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THE RÔLE OF REPRODUCTION IN EVOLUTION¹

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THE establishment of methods of reproduction which maintain variation and inheritance mechanisms on a high plane of efficiency is naturally a fundamental requirement in organic evolution. Since, however, inheritance mechanisms presumably equivalent are common to every method of reproduction, one should be able to interpret the evolutionary tendencies in the matter by comparing their effectiveness in offering selective agencies their raw material. Some will hold this statement to be a self-evident truth; others may maintain as strongly either that the premises are wrong or that the conclusion is not justified even if the premises be granted. Perhaps it is safer to ply the middle course; if the case is not so obvious as a Euclidian axiom, as a compensation rigorous proof may be less difficult.

As a basis for argument, let us sketch the general trend of reproductive evolution in plants and animals.

Ordinarily, one speaks of two types of reproduction among organisms, asexual and sexual. This is a convention that has taken on the dignity of a "folkway" among biologists. Its employment should imply assent to the proposition that the varied forms in which each of these classes presents itself are inherently equivalent, and that

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the groups considered as units are fundamentally distinct, but it is doubtful whether any such implication would be admitted by the majority of its users. In fact one could hardly maintain that simple division, sporification, the production of gemmules, true budding, fragmentation with regeneration of parts, and the various kinds of apogamy and parthenogenesis on the one hand, and all nuclear fusions on the other, can be grouped together as if they are of the same evolutionary value, if this term be used in any narrow or special sense; but from a broader viewpoint, the conventional classification has a real and deep meaning which perhaps the biologist has grasped instinctively.

There are both asexual and sexual methods of reproduction in nearly all groups of animals and plants; among animals the second has almost supplanted the first, among plants the two have continued side by side. In neither kingdom was sex developed as a more rapid means of multiplication, since, as Maupas showed, a single infusorian may become the progenitor of some 50,000 individuals during the time necessary for one pair to conjugate. Some other requirement was fulfilled; and fulfilled adequately if we may judge by the number of times sexual differentiation arose and the tenacity with which it was retained.

Just when sexual reproduction first originated in the vegetable kingdom is still a question. Among the lower forms only the schizophytes, flagellates and myxomycetes have passed it by. Perhaps it is for this reason that these forms have remained the submerged tenth of the plant world. It is tempting, as Coulter (1914) says, to see sex origin in the Green Algæ. There, in certain species, of which *Ulothrix* is a good example, spores of different sizes are produced. Those largest in size germinate immediately under favorable conditions and produce new individuals. Those smaller in size also germinate and produce new individuals, but these are small and their growth slow. Only the smallest are incapable of

carrying on their vegetative functions. These come together in pairs. Two individuals become one as a prerequisite to renewed vigor. Vegetative spores become gametes. Something valuable—speed of multiplication—is given up for a time that something more valuable in the general scheme of evolution may be attained.

This is indeed an alluring genesis of sex. Let us use the indefinite article, however; no doubt it is *a* genesis of sex, but it can hardly be *the* genesis of sex. Various manifestations of sex are present in other widely separated groups of unicellular plants, the Peridineæ, the Conjugatæ and the Diatomeæ—the Conjugatæ being indeed the only great group of plants in which there is no asexual reproduction. In these forms one can not make out such a good case of actual gametic origin, but the circumstantial evidence of sex development in parallel lines is witness of its paramount importance.

After the origin of sex, many changes in reproductive mechanisms occurred in plants, but almost all of them resulted merely in greater protection of the gametes, in increased assurance of fertilization, or in provision for better distribution. First there was a visible morphological differentiation of gametes, the one becoming a large inactive cell stored with food, the other becoming small and mobile. Then came the evolution of various sex organs, and finally the alternation of generations. In the higher plants a long line of changes have occurred connected with the alternation of generations; the spore-producing type has developed from a form of little importance to that which dominates the vegetable world, the gamete-producing type has degenerated until it consists of but two or three cell divisions. In these variations there is reproductive insurance, something which also may be said of those manifold adaptations which provide zygotic protection either in the seed or the adult plant, but they are no more direct changes in reproductive mechanism than are the diverse means which arose to secure dispersal. In fact in all of these changes no new

process of fundamental evolutionary significance occurred, unless it be the various mechanisms devised to promote or to insure cross-fertilization, and which may be interpreted as variations tending to perfect sexuality.

Coincident with the general trend of plant evolution just mentioned, two important changes in the nature of retrogressions occurred, which have persisted in many species. A new type of asexual propagation arose, apogamy, which though it appeared under several guises, apogamy in the narrow sense, parthenogenesis and polyembryony, is none the less asexual reproduction returned under another name and apparently with no particular advantages over the older types. Further, hermaphroditism was developed and has persisted in numerous lines. We may be wrong in calling hermaphroditism a retrogression, for it has the great advantage of a certain economy of effort in the production of gametes, but nevertheless it is certainly a change which *per se* is in the opposite direction from that established when sex was first evolved. A moment of consideration not only makes this clear, but gives us a pretty satisfactory proof that the gain made when continuous multiplication was halted for a time by the intervention of a fusion at the genesis of sexual reproduction was in some way connected with the mixture of dissimilar germplasms. This conclusion is hardly avoidable from the fact that although hermaphroditism retained the cell fusion mechanism of gonochorism it was still necessary for Nature to evolve means for cross-fertilization. And the multitude of ways in which she solved this problem must mean that an immense advantage was secured.

In spite of the great morphological differences between animals and plants, the essential evolutionary changes affecting reproduction in the two kingdoms have been so similar as to be almost uncanny. Accepting the division of animals into twelve phyla as recognized by many modern zoologists (Parker and Haswell), one finds the following facts regarding reproduction. Asexual repro-

duction in the narrow sense is common in Protozoa, Porifera, Cœlenterata and Platyhelminthes, and is sporadic in Molluscoida, Annulata, Arthropoda and Chordata. If fragmentation and regeneration be included, Echinodermata and possibly Nemathelminthes are added. If parthenogenesis is included, Trochhelminthes is admitted. Thus only the Mollusca have no form of asexual reproduction, and zoologists would hardly feel safe in maintaining its absence there since the life history of so many forms is unknown. This being the case, one must admit that asexual reproduction has been found satisfactory for most of the great groups of animals as far as actual multiplication is concerned. For other reasons, however, it evidently did not fulfill all requirements, since sexual reproduction is established in every phylum. Further, omitting the Protozoa in which it is difficult to decide such sexual differences, gonochorism is present everywhere except in the Porifera, and hermaphroditism everywhere except in the Trochhelminthes, although in Nemathelminthes, Echinodermata and Arthropoda it is rare.

Now if our conclusions regarding the true rôle played by sex in evolution are correct, hermaphroditism is a secondary and not a primitive phenomenon. In this we follow Delage, Montgomery and Caullery rather than the majority of zoologists. We believe it to be the only logical view in spite of the fact that the Porifera, usually considered so unspecialized, are all hermaphroditic. Perhaps the Porifera are farther along in specialization than is admitted, for to find the substance nearest chemically to the so-called skeleton of the sponges one must turn to the arthropods (the product[®] of the spinning glands of certain insects). Hermaphroditism, therefore, as in plants, is from this viewpoint a regression. And as in plants it was not found adequate. In giving up diecism for monecism, something was lost, and this something had to be regained by further specialization. Hence, even as in the vegetable kingdom one finds the essential feature of bisexuality, mechanisms providing for mixtures of dif-

ferent germplasms, restored by means of protandry, protogyny or self-sterility.

In even such a brief consideration of the more important changes which have occurred in the reproductive mechanisms of animals and plants, one thing stands out impressively. Both animals and plants have adopted as the most acceptable and satisfactory modes of reproduction, methods which are identical in what we deem to be the essential features, something that can be said of no other life process. These significant features are the preparation of cells which in general contain but half of the nuclear material possessed by the cells from which they arise, which are differentiated into two general classes that show attraction toward each other, and which will fuse together in pairs to form the starting point of a new organism. This parallel evolution is of itself valid evidence of the importance of the process. Let us return to our original proposition for its interpretation.

First, is there any evidence that sexual reproduction differs from asexual reproduction in what may be called the heredity coefficient? In other words, does one method hold any advantage over the other as an actual means for the transmission of characters? I have answered this question in the negative, but it must be confessed that the basis for this answer is a long and intimate experience in handling pedigree cultures of plants rather than the study of a large amount of quantitative data bearing directly on the problem. Quantitative data are to be found, of course, and plants furnish the best material because of the ease in handling large numbers of both clons and seedlings side by side; but even with the best of plant material, several undesired variables are present. Practically the inquiry must take the form of a comparison between the variability of a homozygous race when propagated by seeds and when propagated by some asexual method. The first difficulty is that of obtaining a homozygous race and thus eliminating Mendelian recombination. The traditionally greater variability of seed-propagated

strains is due wholly to this difficulty, I believe. It may be impossible to obtain a race homozygous in all factors. There may be a physiological limit to homozygosis even in hermaphroditic plants. The best one can do is to use a species which is naturally self-fertilized, relying on continued self-fertilization for the elimination of all the heterozygous characters possible. I have examined many populations of this character in the genus *Nicotiana* and have been astounded at the extremely narrow variability they exhibit. Even though one can not grow each member of such a population under identical conditions as to nutrition, the plants impress one as if each had been cut out with the same die. Qualitative characters such as color show no greater variation, as far as human vision may determine, than descendants of the same mother plant propagated by cuttings. Further, in certain characters affected but slightly by external conditions, such as flower size, the sexually produced population not only shows no greater variability than the asexually produced population, but it shows no more than is displayed by a single plant. Yet one must remember that in such a test the seeds necessarily contain but a small quantity of nutrients, and for this reason the individual plants are produced under somewhat more varied conditions than those resulting from cuttings, hence it would not have been unreasonable to have predicted a slightly greater variability for the sexually produced population even though the coefficient of heredity of both were the same.

I have made similar though less systematic observations on wheat—an autogamous plant almost as satisfactory for such a test as *Nicotiana*—with practically identical results. I do not know of any published data on the subject, however, taken either from these or any other plants. In fact, there are few other plants from which data could be obtained with so little likelihood of experimental error.

On the other hand, zoology has furnished a considerable amount of such evidence (*cf.* Casteel and Phillips,

1903; Kellogg, 1906; Wright, Lee and Pearson, 1907). One need only mention Kellogg's work on bees as a type. Kellogg assumed that if amphimixis were the principal cause of the continuous variations postulated by Darwin and Weismann as the most important source of material for the use of the natural selection,² parthenogenetically produced individuals should be less variable than those produced sexually. A statistical investigation showed, however, that the characters of drones probably are more variable than those of worker bees of the same race. Since Kellogg believes Darwin's judgment that "males vary more than females" to have been disapproved, he concludes that "amphimixis is not only not necessary in order to insure Darwinian variation, but there is no evidence (that I am aware of) to show that it increases variation."

It is hardly necessary to point out here the numerous mathematical and biological pitfalls which should be considered before one could accept as valid the statistical differences that appear to exist when coefficients of variation based on such data are examined. It should suffice to note that the researches of Wright, Lee and Pearson (1907) on wasps of the species *Vespa vulgaris* showed just as great a difference in variability between workers and drones in favor of the former. Apparently, the statistics in these two nearly related groups lead to opposite conclusions; in reality probably neither statistical difference is significant as far as the question we are discussing is concerned. The only conclusion justified by such data would seem to be that the coefficient of heredity is as high in the production of asexual as it is in the production of sexual forms.

Moreover, one can not expect anything more definite from this method of attack. Biologists may differ as to

²It should be noted here that all parthenogenetic eggs are not mere spores. Some preparation often occurs through the emission of one polar body. This may be merely a kind of recapitulation, a vestigial process no longer having any significance whatever, but since we are not certain it seems to the writer that the evidence from plants at present must be regarded as stronger.

the definition of fluctuation, mutation, etc., but they are generally agreed that germinal variations, be they great or small, are in most species so rare they can not be gauged by the use of ordinary statistical methods. For this reason, a comparison between the variability of the drones and of the workers of a pure race of bees is not likely to show any difference between these two modes of reproduction in the matter of the frequency or the type of the germinal variation produced, and can not answer the question as to whether sexual reproduction contributes more material for the use of natural selection than asexual reproduction. A study of variability in crossed races, where the effect of Mendelian recombination can be considered, would be a more logical attack upon the second problem, but is hardly necessary in view of the other evidence available.

One is then justified in claiming there is no experimental evidence to show that sexual reproduction in itself is not an exact equivalent of asexual reproduction in the matter of a heredity coefficient, but is this also true for germinal variation? We believe it is. Variations there are in both asexual and sexual reproduction, but it can not be maintained that they occur more frequently in the latter. There are insects in Oligocene amber apparently identical with those of to-day, proving that constancy of type is possible through long periods of time under sexual reproduction; yet germinal variations occur to-day in somewhat noteworthy numbers, as Morgan's work on *Drosophila* shows, although the proportion of these variations which show possibilities of having an evolutionary value, as evidenced by persistence in natural types, is probably small. On the other hand, the number of variations produced under the dominance of asexual reproduction can not be said to be less numerous, even among organisms of a relatively high specialization. If there are those who doubt this statement, let them refer to the immense list of bud-variations in the higher plants compiled by Cramer (1907).

There would be little reason in pushing the claims

further, since even though there does not seem to be a sufficient difference between sexual and asexual reproduction in the matter of variation frequency to make it a subject of experimental proof, certain theoretical points raise the suspicion that there is such a difference. All we would maintain is that to account for the general persistence of sexual reproduction by such a cause, the difference in its favor should be so great that it could easily be determined experimentally. Since this is not true, we believe the hypothesis should be discarded.

The points of theory referred to are these. It will be allowed by all that there is some considerable evidence of the chromosomes being the most important conservators of hereditary factors—the physical bases of heredity in whatever form they may be. If it is assumed then that changes in constitution in these cell organoids are followed by changes in type, and that such changes in constitution are equally probable in all chromosomes, it follows that parthenogenetic individuals having the haploid number of chromosomes should show a larger proportion of germinal variations than members of the same species having the diploid number of chromosomes, because variations of all kinds should be recognizable in the former case, while in the latter, recessive variations could not be detected until the first or second filial generation, and then only when the proper mating was made. There is some evidence that this reasoning is not wholly improbable. But variations occur much more frequently in heterozygotes than in homozygotes. To me this simply means that bud-variations *are detected* more frequently in heterozygotes than in homozygotes: and an interpretation is not hard to find. Retrogressive variations are much more frequent than progressive variations, and a retrogressive variation in a particular character shows only when the organism is heterozygous for that character. If a retrogressive bud-variation arises in a homozygote and gametes are afterwards developed from the sporting branch it is not at all unlikely that the variation may show in the next generation, but it will be attributed then to

gametic mutation. If one compares asexual and sexual reproduction from the standpoint of frequency of variation only, then sexual reproduction may seem to hold the advantage over asexual reproduction in the usual sense; but parthenogenesis, which is certainly a form of asexual reproduction, is in theory better adapted than sexual reproduction for giving large numbers of variations.

If, therefore, one is constrained to agree that the bulk of the evidence points to a practically identical coefficient of heredity for both forms of reproduction, and that variation in the sense of actual changes in germinal constitution *may* occur with greater frequency in asexual reproduction, if there is any difference at all between the two forms, he is driven either to the conclusion of Maupas that continued asexual reproduction is impossible through some protoplasmic limitation or to the conclusion of Weismann that a mixture of germplasms offers sufficient advantages to account for everything. This is the dilemma³ unless one wishes to maintain that efficient mechanisms for nutrition, adaptation, protection and distribution could not be evolved or maintained under asexual reproduction.

The contention of Maupas can not be dealt with experimentally any more successfully than the question as to the inheritance of acquired characters since experimental time and evolutionary time are not of the same order of magnitude. The long-continued experiments of Woodruff in which vigorous strains of paramecium have been kept dividing asexually for several thousand generations, however, as well as the botanical evidence that numerous species having no sexual means of multiplication have continued to exist during long periods of time, weight the balance against him. One need not hesitate to concede that all of these organisms are rather low unspecialized types; the modern development of genetics has built up such a solid structure in favor of Weismann's view that there is little need of argument along the older line.

³ Naturally another hypothesis wholly new to biology may be submitted at any time.

The main argument in favor of Weismann's viewpoint does not take long to state. It is this: Mendelian heredity is a manifestation of sexual reproduction. Wherever sexual reproduction occurs, there Mendelian heredity will be found. The very fact that it describes the sexual heredity of both animals and plants is sufficient proof of its generality in this regard. Now if N variations occur in the germplasm of an asexually reproducing organism, only N types can be formed to offer raw material to selective agencies. But if N variations occur in the germplasm of a sexually reproducing organism 2^N types can be formed. The advantage is almost incalculable. Ten variations in an asexual species mean simply 10 types, 10 variations in a sexual species mean the possibility of 1,024 types. Twenty variations in the one case is again only 20 types to survive or perish in the struggle for existence; 20 variations, in the other case, may present 1,032,576 types to compete in the struggle. It is necessary to hedge the argument by pointing out that these figures are the maximum possibilities in favor of sexual reproduction. It is improbable that they ever actually occur in nature, for 2^{20} types really to be found in the wild competing for place after only 20 germinal variations would mean an enormous number of individuals even if the 20 changes had taken place in different chromosomes, and if the variations were linked at all closely in inheritance the number required would be staggering. But there are breaks in linked inheritance, and the *possibility* is as stated.

These advantages remain even though it should be shown later that the more fundamental and generalized characters of an organism are not distributed by Mendelian heredity. Loeb (1916) believes that the cytoplasm of the egg is roughly the potential embryo and that the chromosomes, distributed as required by the breeding facts of Mendelian heredity, are the machinery for impressing the finer details. There is something to be said for this point of view, though at present it is but a working hypothesis. But granting its truth it does not detract from the advantages gained by sexual reproduction. Even the most

strict mutationist would hardly maintain that evolution in general has come about through tremendous changes involving sterility between the mutant and the parent types. It seems unnecessary to deny such possibilities; but the weight of evidence is in favor of the majority of variations being comparatively small, changes in detail, the very kind which are known to be Mendelian in their inheritance.

Yet sexual reproduction in itself does not assure these advantages, though they are based upon it. There must be means for the mixture of germplasms. This opportunity was furnished originally by bisexuality. Then came hermaphroditism, manifestly an economic gain, yet on the whole unsuccessful except as functional bisexuality was restored by self-sterility, protandry, protogyny or mechanical devices which promoted cross-fertilization.

The prime reason for the success of sexual reproduction then, as Weismann maintained, is the opportunity it gives for mingling germplasms of different constitution and thereby furnishing many times the raw material to selective agencies that could possibly be produced through asexual reproduction. Further, there are three minor advantages which rest upon the same mechanism. They are minor advantages only when compared to the major, and should not be passed by.

Let us first consider heterosis, the vigor which accompanies hybridization. This phenomenon has long been known. It is characteristic of first generation hybrids both in the animal and vegetable kingdoms. It affects the characters of organisms in much the same manner as do the best environmental conditions. In other words, the majority of characters seem to reach the highest development in the first hybrid generation. The hybrid individual therefore holds some considerable superiority over the individuals of the pure races which entered into it, and is thereby the better enabled to survive and to produce the multiplicity of forms which its heterozygous factors make possible. The frequency of this phenomenon, for it is almost universal, together with the fact

that it seems impossible to fix the condition, led Shull and the writer independently to the conclusion that certain factors in addition to their functions as transmitters of hereditary characters also had the faculty of carrying some sort of a developmental stimulus when in the heterozygous condition. The recent work of Morgan on linked characters, however, makes it possible to give another interpretation, as Jones (1917) has demonstrated. If it be assumed that several variations have occurred in each of one or more chromosomes, then it can be shown that the first-generation hybrid between such a variant and the race from which it arose will bring together all dominant or partially dominant characters. In the second hybrid generation, on the other hand, Mendelian recombination steps in and makes it improbable that many individuals shall have such a zygotic composition. And only in the rare cases where the proper breaks in linkage have occurred can a homozygous individual of this type be produced.

The latter hypothesis holds the advantage that it furnishes hope for a homozygous combination as valuable as that of the first hybrid generation no matter how rarely it may be assumed to occur, but whether it holds for the majority of organisms or not may depend on a future decision as to the frequency of side-by-side synapsis as compared to end-to-end synapsis. Our knowledge of linkage rests almost entirely on Morgan's work on *Drosophila* where side-by-side synapsis occurs at the maturation of the germ cells. If the break in linkage between groups of characters apparently carried by a single chromosome, which Morgan finds to be so exact in *Drosophila*, should actually depend on Jannsen's theory of chromosome, twisting at synapsis, then some other type of inheritance may be found in species having end-to-end synapsis. Perhaps this is the reason why the *Oenotheras* have such a peculiar heredity, for in them Davis (1909) thinks end-to-end synapsis prevails. But, be this as it may, the vigor of first generation hybrids is a fact and not a theory, and the advantage it brings to the hetero-

zygotic individual in competition with its fellows can not be gainsaid.

The investigations of Shull and of the writer on the effects of cross- and self-fertilization have brought to light another series of facts with a bearing on the problem under discussion. It has been shown that the apparent deterioration of cross-bred species when self-fertilized is in large measure and perhaps wholly due to the loss of hybrid vigor⁴ through the formation of homozygotic Mendelian recombinations and not an effect of inbreeding *per se* because of the union of like germplasms. This is a plausible argument against Darwin's idea that continued inbreeding is abhorrent to Nature. It may even be said to be a valid reason for declining to accept Maupas's belief in the impossibility of continued asexual reproduction, for there is no very good reason for distinguishing between continued asexual propagation and continued self-fertilization. Inbreeding simply brings about the opposite effect from crossing, and we can see no reason for the comparative failure of naturally inbred types in the wild other than the lack of chances for progress. The one is the conservative manufacturer who continues the original type of his article, the other is the progressive who makes changes here and there without discouragement until the acceptable improvement is found. In fact, if this argument be overlooked, the inbred types which have persisted hold some advantages over the cross-bred types. The self-fertilized species are inherently strong and vigorous, witness tobacco and wheat. They stand or fall on their own merits. They are unable, as are cross-bred species, to cover up inherent weakness by the vigor of heterozygosis. Cross-fertilized maize has become the king of cultivated plants because of its variability, but many of our best varieties carry recessive characters very disadvantageous to the species.

The next secondary advantage of sexual reproduction is

⁴ Accepting the view that the vigor of the first hybrid generation is due to dominant characters meeting makes this argument even more forcible.

the division of labor made possible by secondary sexual characters, using the term very generally and including even such differences as those which separate the egg and the sperm. It is not known just how these differences arose or by what mechanism they are transmitted. The greatest hope of reading the riddle lies in an investigation of hermaphroditic plants, for there are technical difficulties which seem to preclude their solution in animals. For example, breaks in the linkage between sex-linked characters occur only in the female in *Drosophila*, and as the sex chromosome is double in the female, it can not be determined whether the differentiation between male and female is due to the whole chromosome or not. But this ignorance does not give reason for a denial of the great advantage which sexes bearing different characters hold over sexes alike in all characters except the primary sex organs.

The only glimpse of the truth we have on these matters comes from recent work on the effect of secretions of the sex organs on secondary sexual characters. The effect of removing the sex organs and the result of transplanting them to abnormal positions in the body have shown that in vertebrates the secretions of these organs themselves activate the production of the secondary sexual characters. This does not seem to be the case in arthropods, however, so one can not say that primary sexual differentiation and secondary sexual differentiation is one and the same thing.

Finally there is a presumable advantage in gonochoristic reproduction in having sex-linked characters. We say presumable advantages, for all of the relationships between sex and sex-linked characters are not clear. The facts are these: One sex is always heterozygous for the sex determiner and the factors linked with it. Now it may very well be that there is an actual advantage in the heterozygous condition, as we have seen above. But should the so-called vigor of heterozygosis prove to be only an expression of the meeting of dominant characters, still a possible advantage accrues to this phenomenon be-

cause the mechanism contributes toward mixing of germ-plasms. As an example, let us take the *Drosophila* type of sex determination. There the sperm is of two kinds: the one containing the sex chromosome and its sex-linked factors, the other lacking it. The eggs are all alike, each bearing the sex chromosome. It follows then that the male *always* receives this chromosome from his *mother*, who may have received it from *either* her *father* or *mother*. Moreover, further variability may be derived from the linkage breaks which occur always in the female. This last phenomenon is hardly worthy of special mention, however, until it is shown to be typical of such reproduction.

This short reconnaissance presents the pertinent facts in the situation as they appear to the writer. A very great number of interesting things connected with reproduction during the course of evolution have not been mentioned. This is because it is felt that the essential feature of the rôle of reproduction in evolution is the persistence of mechanisms in both the animal and plant kingdoms which offer selective agencies the greatest amount of raw material. Other phenomena are wholly secondary.

LITERATURE CITED

- Casteel, D. B., and Phillips, E. F. 1903. Comparative Variability of Drones and Workers of the Honey Bee. *Biol. Bull.*, 6: 18-37.
- Coulter, J. M. 1914. The Evolution of Sex in Plants. Chicago, University of Chicago Press. Pp. 1-140.
- Cramer, P. J. S. 1907. Kritische Übersicht der bekannten Fälle von Knospenvariation. *Natuurkundige Verhandelingen van de Hollandse Maatschappij der Wetenschappen. Derde Verzameling, Deel VI, Derde Stuk.* Haarlem, De Erven Loosjes, pp. iii-xviii + 474.
- Davis, B. M. 1909. Cytological Studies on *Oenothera*. I. *Ann. Bot.* 23: 551-571.
- Jones, D. F. 1917. Dominance of Linked Factors as a Means of Accounting for Heterosis. *Genetics*, 2: 466-479.
- Kellogg, V. L. 1906. Variation in Parthenogenetic Insects. *Science*, N. S., 24: 695-699.
- Loeb, J. 1916. The Organism as a Whole. N. Y., Putnam. Pp. v-x + 379.
- Wright, A., Lee, A., and Pearson, K. 1907. A Cooperative Study of Queens, Drones and Workers in *Vespa vulgaris*. *Biometrika*, 5: 407-422.